

# Movement of the Epiglottis in Mammals

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**ABSTRACT** In contrast to adult humans, the epiglottis of other mammals and infant humans is situated close to the soft palate. It has been argued that this posture is maintained during swallowing, with food passing laterally around an intact airway. To test this supposition, the movement of the epiglottis in two contrasting mammalian species, pigs and ferrets, was studied by placing radiopaque markers on the epiglottis and soft palate. Swallowing was observed with videofluoroscopy while the animals were feeding on hard and soft foods, liquids, and food mixed with barium sulfate. Analysis of the images showed that bolus formation and downward movement of the epiglottis away from the soft palate were unvarying phenomena in both animals for all tested foods. The duration of the epiglottic movement was approximately 0.3 s for liquids and slightly longer for solids. Because swallowing never occurred past an upright epiglottis, the results of this study do not support the hypothesis that adult animals maintain a patent airway during swallowing. Instead, the epiglottis in nonhuman mammals downfolds similarly to that of adult humans during swallowing. © 1996 Wiley-Liss, Inc.

Many years ago Negus (1949, 1965) pointed out that the spatial positioning of the adult human larynx is uniquely different from that found in other mammals. In non-human mammals and in human infants the larynx is located high in the neck, and the epiglottis is in close proximity to the soft palate. Indeed, in many mammals, especially ungulates, the epiglottis at rest lies on the posterior side of the soft palate, well into the nasopharynx. Negus's interpretation of this typical mammalian anatomy was that the epiglottis serves to link the nasopharynx and larynx for the purpose of olfaction (1949). He further stated that this arrangement allowed swallowing, at least of liquid or semisolid foods, to occur around the upright epiglottis while respiration proceeds uninhibited (1949, 1965). Later workers have generally agreed with this interpretation (Laitman et al., 1977; Crelin, 1987) and have expanded on the implications of the low position of the larynx and epiglottis in adult humans, pointing out that the resultant cross-

ing of digestive and respiratory pathways puts the airway at risk during swallowing. As a secondary consequence, the epiglottis is said to have lost its original role in separating the two pathways; instead, it folds backwards during swallowing to help protect the airway (Laitman and Reidenberg, 1993). Offsetting the disadvantage to the respiratory pathway, the adult human condition has been construed as an adaptation for producing certain sounds, including essential vowels, critical for speech (Lieberman et al., 1972; Laitman and Heimbuch, 1982).

The scenario summarized above has many heuristic features and is widely accepted in anthropological circles. It implies a revolutionary reorganization of the mammalian coordination of respiration and feeding in the

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genus *Homo* and furthermore that this reorganization is recapitulated in the postnatal ontogeny of every human. Moreover, there is strong evidence for certain elements of the scenario. In particular, the difference in resting posture of the hyolaryngeal apparatus between adult humans and other mammals (including human infants) is well documented (references above; Sasaki et al., 1977; Laitman and Crelin, 1980), as is the downfolding of the epiglottis during adult human swallowing (Mosher, 1927; Johnstone, 1942; Saunders et al., 1951; Rushmer and Hendron, 1951; Ardran and Kemp, 1952; Ramsey et al., 1955; Fink and Demarest, 1978; Ekberg and Sigurjonsson, 1982).

However, data are contradictory for other aspects of the scenario. Two areas are especially problematic. First, the coordination of respiration and swallowing in nonhuman mammals (and human infants) appears to be identical to adult humans in that respiration is inhibited during swallowing (dogs: Bosma, 1957; Biewener et al., 1985; rabbits: McFarland and Lund, 1993; human infants: Wilson et al., 1981; Kenny et al., 1989; Koenig et al., 1990; Selley et al., 1990; Kramer and Monahan-Eicher, 1993). Thus, even if an upright epiglottis makes it possible for animals to breathe and swallow simultaneously, they do not do so. Physiologically, then, no revolutionary reorganization of the coordination of breathing and swallowing occurred in the evolution of the genus *Homo*.

Second, the role of the nonhuman epiglottis during swallowing is debated. A few reports argue that the epiglottis does not in fact remain upright during swallowing but folds down just as in adult humans (lambs and kid goats: Ardran et al., 1958; pigs: Herring and Scapino, 1973; infant humans: Ardran et al., 1958; illustrations in Bosma et al., 1965). This point of view is reflected in most veterinary texts (e.g., Nickel et al., 1973). The case for an upright epiglottis was made for infant humans by Peiper (1963; based on an unpublished study by Dittrich, 1957) and more recently by Crelin, Laitman, and their colleagues. In studies on young macaques with radiopaque markers on the epiglottis (Laitman et al., 1977) and human infants (Laitman et al., 1977; Sasaki et al., 1977), these workers observed momentary

unlocking of the epiglottis from the soft palate in most swallows (the exceptions were some water (monkey) and saliva (human infant) swallows). Although these brief movements were not described, the upright condition of the epiglottis is implied by the statements that liquid and soft boluses "pass around the interlocked larynx via the fauces en route to the esophagus" (Laitman and Crelin, 1980:15) and that in nonhuman mammals "The connection between the epiglottis and the soft palate may only be broken during some vocalizations, swallowing of a large bolus of food, or with disease" (Laitman and Reidenberg, 1993:321). If this is so, then there is still a fundamental difference between adult humans and all other adult mammals in the performance of swallowing, indicating that an important reorganization of functional morphology (although not of coordination) did in fact occur.

The purpose of the present study is to address this second problem. We ask whether the momentary deflections of the nonhuman epiglottis during swallowing constitute a downfolding over the airway equivalent to the movement seen in the adult human or whether the epiglottis remains largely erect, maintaining a patent airway during swallowing. Using radiopaque markers, we describe epiglottic movement during swallowing in two mammalian species, the pig (*Sus scrofa*), an artiodactyl ungulate, and the ferret (*Mustela putorius furo*), a carnivoran. These species were selected to represent the expected extremes of epiglottic function. Pigs like other ungulates have a large intranarial epiglottis of the sort that Negus (1949) expected to remain upright during swallowing and to direct the semiliquid bolus around its sides. Carnivorans such as the ferret have a somewhat smaller epiglottis than ungulates, and at rest it may be either intranarial or intraoral (Negus, 1949; Biewener et al., 1985). Because carnivores typically swallow large solid boluses, Negus (1949) postulated that their epiglottis would be forced downward by pressure of the bolus. Although such a movement would resemble the downfolding of the adult human epiglottis, Negus viewed it as a secondary, passive act and not protective of the glottis. Based on the literature, therefore, we hypothesized

that the epiglottis of the pig would remain upright during all swallows, whereas the epiglottis of the ferret would do so only during swallows of liquid.

### MATERIALS AND METHODS

The sample consisted of three young female Hanford miniature pigs (Charles River Labs, Wilmington, MA) weighing between 25 and 35 kg and two adult male ferrets (Marshall Farms, North Rose, NY) weighing between 1.25 and 2.0 kg. Two of the pigs (pigs 2 and 3) had been used in a previous experiment involving mandibular reconstruction. They had fully recovered from the earlier surgery, and the normality of their feeding behavior was verified by electromyography and videorecording. All pigs were fed pig chow pellets. One pig (the one not used in the previous experiment) was also fed solid and liquid food mixed with barium sulfate. One ferret was fed ferret chow pellets and water, while the other would eat only ground turkey mixed with barium sulfate. The pigs ate from a feeding stand, and the ferrets ate in a radiolucent feeding box.

Pigs were anesthetized using 1–3% halothane in a 50/50 mixture of nitrous oxide and oxygen administered by mask. The mask was removed for marker placement, which was aided by laryngoscopy. Ferrets were anesthetized with Ketamine (25 mg/kg IM) and Xylazine (1 mg/kg IM). Atropine (0.10 mg/kg IM) was sometimes used to control salivary secretions. This regimen produced a light stage of anesthesia for approximately 30 min during which laryngoscopy allowed marker placement.

Epiglottic markers were U-shaped clips which were compressed with a special instrument. The pig clips were formed from 0.8 mm stainless steel, approximately 4.0 mm × 6.0 mm before compression, whereas the ferret markers were stock tantalum hemoclips (0.5 mm thickness), which formed a loop approximately 4 mm long after compression. The markers were positioned on the free edge of the epiglottis near the median plane. The soft palate markers consisted of 3–4 mm sections of either 0.8 mm round or 0.5 mm × 0.6 mm rectangular stainless steel wire. These sections of wire

were injected into the submucosal tissue of the soft palate by being placed into the lumen of a hypodermic needle and then forced out with a wire attached to the plunger of the syringe. An attempt was made to place the marker in the median plane as close to the free margin of the soft palate as possible. The ferrets were radiographed after marker placement to verify proper positioning.

After a recovery period of at least 24 h, during which time normal eating patterns returned, the animals were observed fluoroscopically in lateral view while feeding. Video images (30 frames/s) with a time overlay were recorded from a portable Siemens fluoroscopy unit coupled to a high resolution Panasonic monitor. A total of 132 swallows for the pigs and 99 swallows for the ferrets were visualized. At the conclusion of the experiments the animals were euthanized, and dissections were made to clarify anatomical relationships and document marker position.

In general, structures were easier to visualize on the much larger pigs. At rest and during chewing, all markers were visible except (usually) the soft palate marker in the ferrets, which was obscured by the superimposition of cranial base structures. Hence, we did not analyze the movements of this marker.

To analyze swallowing movements, markers and anatomical landmarks were digitized frame by frame and plotted (Peak 2D and Peak 5 programs; Peak Performance Technologies, Englewood, CO). Barium swallows often obscured the markers. Analysis was based on swallows in which at least the epiglottic marker was clear: 83 pig swallows (from three animals) and 44 ferret swallows (from one animal). Sequences selected for detailed motion analysis were those with minimal head movement and good outlines of all bony structures as well as faint outlines of the epiglottis, thyroid cartilage, tongue, and soft palate. In the pig the movements of the soft palate and epiglottic markers were referenced against the most ventral point on the ventral arch of the atlas and the most caudal, ventral point on the body of C-2 (Fig. 1). In the ferret the smaller size of the head permitted the use of skull points as references, the most posterior, superior point of

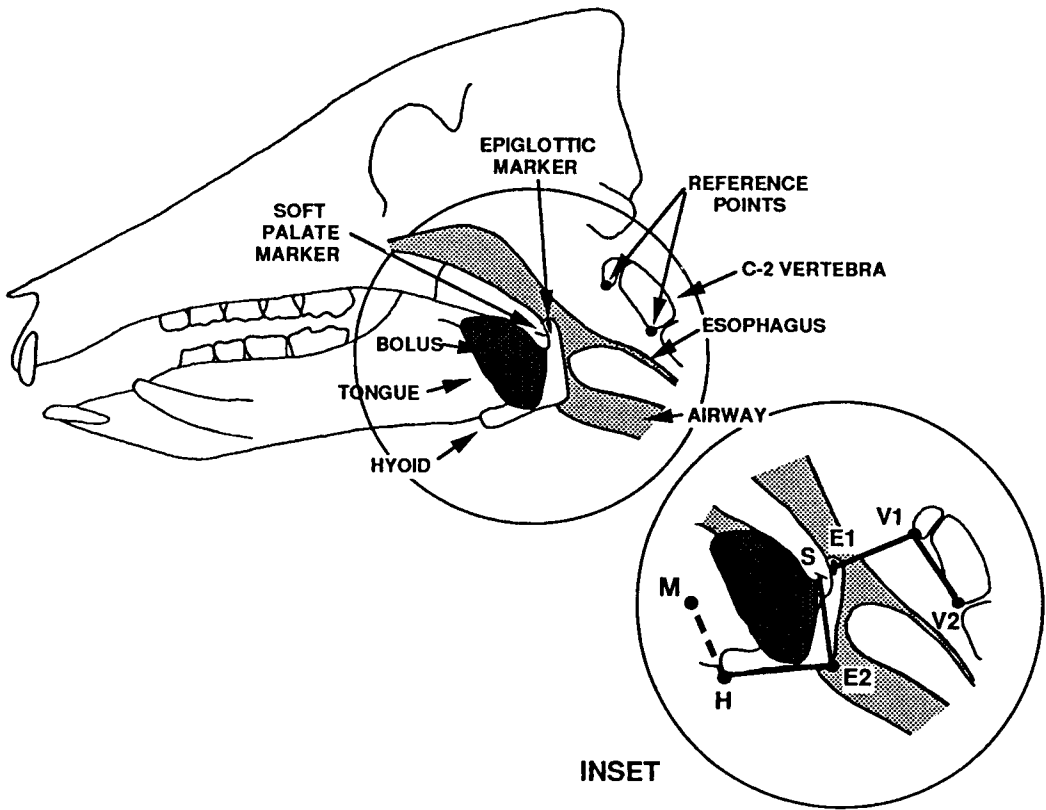


Fig. 1. Sagittal section of the pig drawn schematically to show structures seen during videofluoroscopy. The airway and entrance to the esophagus are lightly shaded; the bolus, accumulated at the back of the tongue, is darkly shaded. The inset shows a superimposition of the points digitized and the lines used to construct

computer-generated figures. E1, epiglottic marker; E2, base of epiglottic cartilage; H, anterior extremity of hyoid bone; M, mandibular implant (figs 2 and 3); S, soft palate marker; V1 and V2, vertebral points used as references.

the occipital bone and the most anterior point of the nasal bone (Fig. 2, S1 and S2).

To time the events of swallowing, epiglottic movement was divided into three intervals. The first time interval was the descent time of the epiglottis, defined as the frame just prior to initiation of the swallow to the frame when the epiglottic marker first became visible in the downward position. The second interval, the time spent by the epiglottis in the downward position, was taken from the first frame in this position to the frame just prior to its ascent. The third interval, the ascent time, was taken from this last frame to the first frame in which the epiglottis was erect. Means and standard deviations were calculated for the time intervals observed. Because preliminary exami-

nation indicated that the data were not normally distributed, both parametric (Student's *t*, ANOVA) and nonparametric (Mann-Whitney-U, Kruskal-Wallis ANOVA) (Siegel and Castellan, 1988) tests were used (SPSS for Windows). Parametric and nonparametric tests usually produced the same probability estimates. In the few cases with disagreement, the higher *P* value is reported (Tables 1, 2) in order to minimize type II errors.

## RESULTS

### Anatomy

In contrast to the adult human condition, in which the epiglottis lies well below the level of the dorsum of the tongue, in both pig and ferret (Figs. 1, 2) the entire epiglottic

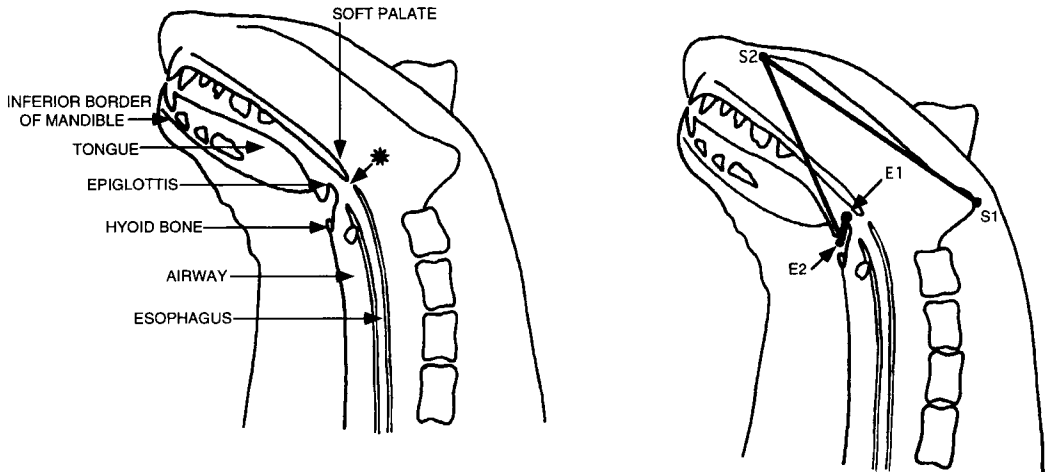


Fig. 2. A sagittal section of the ferret is shown on the left. The asterisk indicates the nasopharyngeal orifice. The sketch on the right shows the points digitized and the lines used to construct computer-generated figures. E1, distal end of epiglottic marker; E2, proximal end of epiglottic marker; S1 and S2, reference skull points.

TABLE 1. Duration of swallows and interval between swallows<sup>1</sup>

	Pig 1	Pig 2	Pig 3	Ferret 1	Ferret 2
Duration					
Liquid	0.29 ± 0.03, 33 <sup>2</sup>	—	—	0.28 ± 0.08, 31 <sup>2</sup>	—
Soft chow	0.35 ± 0.09, 59	—	—	—	—
Hard chow	0.34 ± 0.05, 10 <sup>3</sup>	0.55 ± 0.14, 10	0.52 ± 0.13, 20	0.40 ± 0.10, 13	—
Interval					
Liquid	0.62 ± 0.13, 33	—	—	0.68 ± 0.39, 31	—
Soft chow/turkey	8.88 ± 3.91, 36	—	—	—	6.84 ± 2.43, 46
Hard chow	11.67 ± 4.23, 6	—	15.55 ± 0.85, 2	7.44 ± 2.99, 46	—

<sup>1</sup> All results are given as mean(s) ± SD, N.

<sup>2</sup> Significantly different from other foods for this animal,  $P < 0.01$ .

<sup>3</sup> Significantly different from other pigs,  $P < 0.01$ .

TABLE 2. Time intervals for epiglottic movement<sup>1</sup>

	Pig 1	Pig 2	Pig 3	Ferret 1
Liquid				
D	0.10 ± 0.04, 23	—	—	0.07 ± 0.02, 31 <sup>5</sup>
T	0.12 ± 0.05, 23	—	—	0.07 ± 0.02, 31 <sup>5</sup>
A	0.06 ± 0.03, 23	—	—	0.13 ± 0.03, 31 <sup>5</sup>
Soft Chow				
D	0.07 ± 0.02, 21	—	—	—
T	0.15 ± 0.03, 21	—	—	—
A	0.07 ± 0.01, 21	—	—	—
Hard Chow				
D	0.10 ± 0.04, 10 <sup>2</sup>	0.16 ± 0.02, 9	0.18 ± 0.04, 20	0.15 ± 0.04, 14 <sup>3</sup>
T	0.13 ± 0.05, 10	0.20 ± 0.10, 8	0.20 ± 0.12, 20	0.09 ± 0.01, 13 <sup>3,5</sup>
A	0.11 ± 0.04, 10 <sup>3</sup>	0.21 ± 0.10, 8 <sup>4</sup>	0.14 ± 0.06, 20	0.16 ± 0.05, 13 <sup>6</sup>

<sup>1</sup> D, descent time; T, time in descended position; A, ascent time. Mean (sec) ± s.d., N.

<sup>2</sup> Significantly different from other pigs,  $P < 0.001$ .

<sup>3</sup> Significantly different from other foods for this animal,  $P < 0.001$ .

<sup>4</sup> Significantly different from other pigs,  $P < 0.05$ .

<sup>5</sup> Significant difference between pig and ferret,  $P < 0.01$ .

<sup>6</sup> Significantly different from other foods for this animal,  $P < 0.05$ .

cartilage was above this level. In the pig the epiglottis projected cylindrically from the superior aspect of the larynx; its rounded free margin lay for more than a centimeter of its length upon the dorsal surface of the soft palate. This posture was observed radiographically in living animals as well as in cadaver dissections. During marker placement the soft palate had to be pushed far superiorly to allow the epiglottis to move from the nasal cavity to the oral cavity. Its resting position is thus intranarial, as in other ungulates.

In the ferret the epiglottis was seen below the level of the hard palate and thus probably below the soft palate as well (i.e., intraoral) (Fig. 2). However, the pointed tip of the epiglottis could easily have fit through the restricted nasopharyngeal orifice (2–3 mm diameter). Indeed, postmortem, the epiglottis was found intranarially in one ferret and intraorally in the other (and in two cadavers that were dissected for practice). Thus, the resting position of the epiglottis probably varies, as has been reported for dogs (Biewener et al., 1985).

In pigs and ferrets (as well as humans) the epiglottis is closely related to the larynx and particularly to the hyoid bone. Pigs and ferrets have hyoepiglottic muscles in addition to hyoepiglottic ligaments (Sisson and Grossman, 1953). Presumably, movements in these structures would be transmitted to the epiglottis.

### Movements

To ingest liquids, the animals either lapped (ferrets) or sucked (pigs). Solid foods were taken in with the anterior dentition (ferrets) or tongue (pigs). During ingestion and during mastication of soft and hard foods, the epiglottis remained upright and in contact with either the dorsal (pigs) or ventral (ferrets) side of the soft palate. With the rest of the hyolaryngeal apparatus, the epiglottis moved in regular cycles during ingestion and chewing.

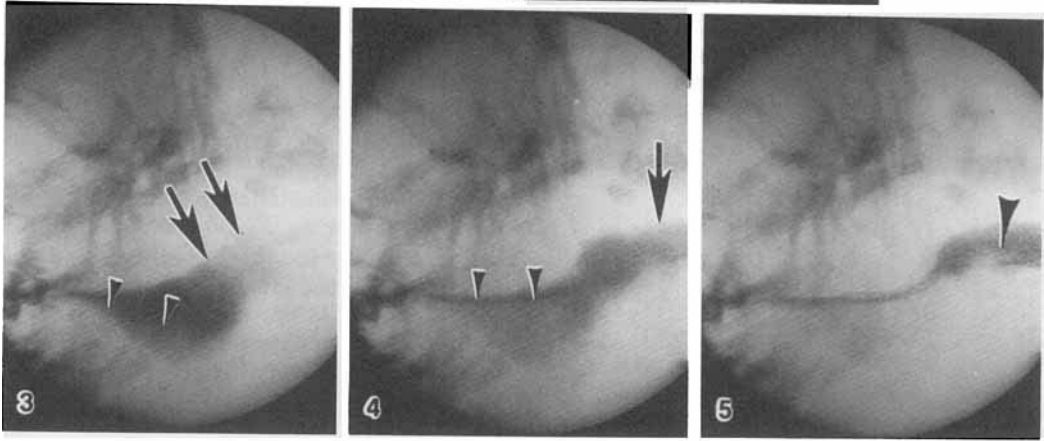
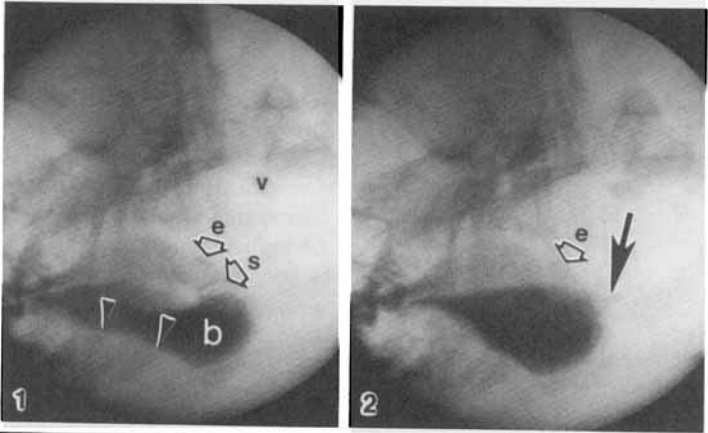
Bolus formation was an unvarying phenomenon for liquids as well as soft and hard solids. In the pig boluses of food were formed in a space bounded by the posterior dorsum of the tongue, the anterior surface of the soft palate, and the anterior surface of the

epiglottis. The area of bolus formation was similar in the ferret, but the exact boundaries of the space could not be well defined. "Streaming" of material past an upright epiglottis that locked into place with the soft palate was never seen. Swallowing was always a distinct event involving the mass transfer of the bolus. However, in pig 1 we occasionally observed that swallowing of barium liquid commenced with a small spurt of material laterally past the upright epiglottis (Fig. 3). Nevertheless, in subsequent frames the epiglottis moved away from the intranarial position, and the main part of the bolus appeared to travel dorsally over the epiglottis rather than in the lateral food channels (Fig. 3), as in the other observed swallows.

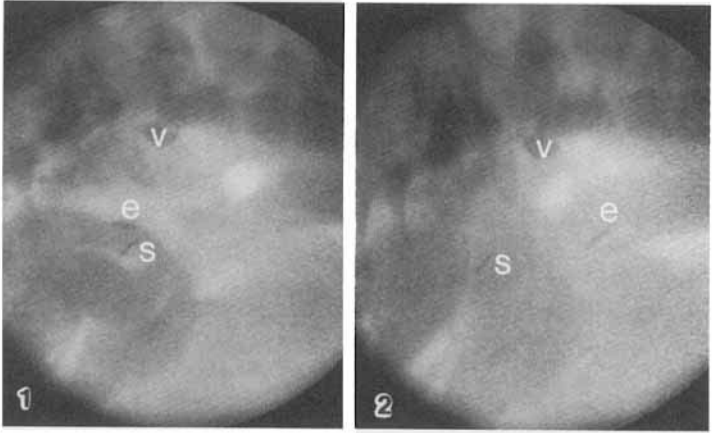
The epiglottis was moved out of its upright position in each of the 176 analyzable swallows observed in the two species. These sequences showed unmistakably that all swallows involved a dramatic descent of the epiglottis, simultaneous with the passage of the bolus through the fauces (Figs. 3–6). There was no difference in the nature of epiglottic movement for foods of different consistencies. The upright epiglottis swung through an arc of greater than 90 degrees as

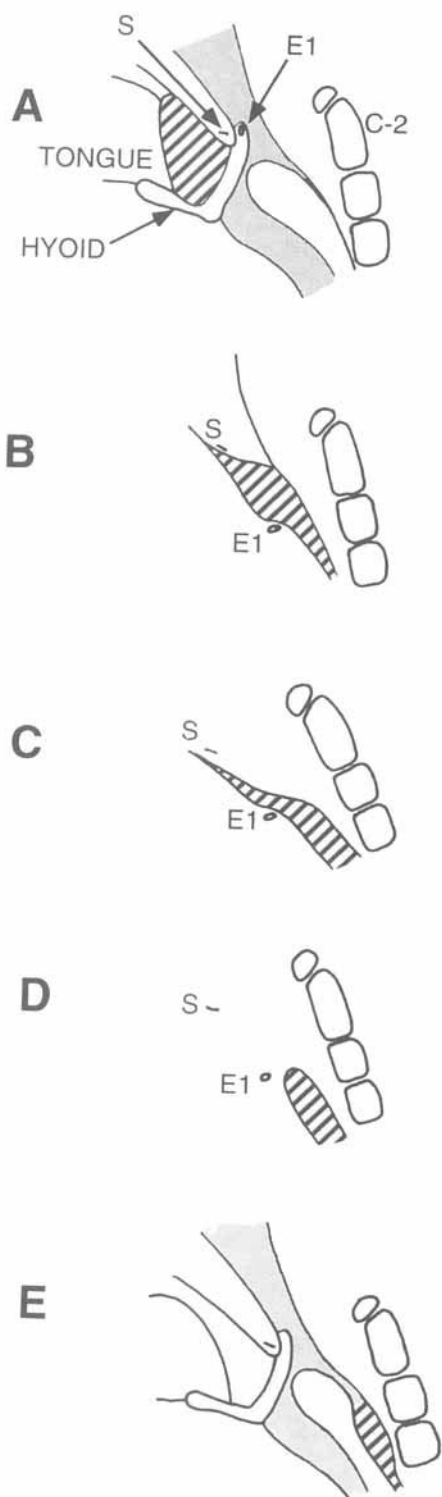
Fig. 3. Photographs of the video monitor illustrating liquid swallowing in pig 1. **A1–A5:** Successive frames from a barium sequence. In A1 fluid is being added to the bolus (b), which is bounded anteriorly and ventrally by the tongue (outlined by arrowheads). The soft palate (marker s) and epiglottis (marker e) are in their usual posture anterior to the atlas (v). In A2 the swallow begins with the epiglottis (marker e) still erect, but with a small extension of the bolus (black arrow) crossing it laterally. In A3 the epiglottic marker is obscured by the bolus (black arrows), which is now passing dorsally as well as laterally; the profile of the tongue (arrowheads) becomes less concave. A4 shows the bolus (black arrow) entering the esophagus dorsally; the profile of the tongue (arrowheads) is almost flat. In A5 the bolus is entirely within the esophagus, and the shadow of the ascending epiglottis can be seen (large arrowhead). Note that the tip of the epiglottis is well posterior to the atlas. **B1, B2:** Two frames from a swallow of liquid without barium to illustrate marker movements. B1 is just before the swallow and is comparable to A1. In B2, about 0.15 s later, the epiglottis is fully depressed. Note that not only has the marker e moved well posterior to the atlas (v) but that it has rotated about 90°. In contrast, the soft palate marker (s) has moved very little; the epiglottis and soft palate are now widely separated.

A



B





it descended. Continuity with the soft palate was lost.

Soft palate movements (observed only in pigs) were less impressive (Fig. 5). Just before or concurrent with the descent of the epiglottis and passage of the bolus, there was a thickening of the soft palate with a slight dorsal movement of its free edge. The occlusion of the nasopharyngeal airway appeared to be more a function of the bulging of the soft palate and the posterior pharyngeal wall than an actual movement. After the bolus had passed, the soft palate returned ventrally, occupying the space vacated by the bolus. The return of the soft palate was typically within one frame (0.03 s) of the ascent of the epiglottis.

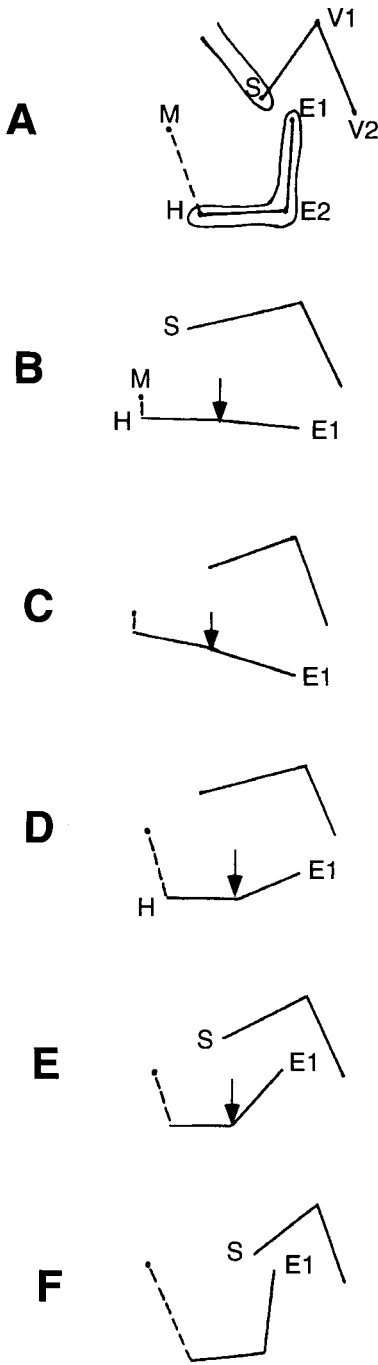
In pig 3, which had a mandibular implant, we digitized the movements of the hyoid and mandible. During chewing and sucking, the hyoid and the epiglottis moved anteroposteriorly in synchrony. This parallelism was lost during swallowing (Fig. 5). As the epiglottis began its descent, the hyoid, accompanied by the rest of the larynx, ascended towards the mandible. When the epiglottis reached its downmost position, the hyoid was at or near its most elevated position.

### Timing

Data on swallowing duration and the interval between swallows (time from the end of one swallow to the beginning of the next) are presented in Table 1. In addition to the evaluation of species differences, individual differences could be assessed for the three pigs eating hard chow, and differences due to food texture could be assessed for two individuals, pig 1 and ferret 1. We did not examine the order of swallows within a feeding

Fig. 4. Tracings of selected frames from pig 1 swallowing liquid mixed with barium. C-2, axis; E1, epiglottic marker; S, soft palate marker. **A:** Immediately prior to initiation of the swallow, a bolus (diagonal hatching) has formed in the space bounded by the tongue, soft palate, and epiglottis. **B:** Three frames (0.10 s) later the epiglottis is downturned, and the bolus is flowing over it. **C:** At 0.15 s the bolus continues flowing past the downturned marker. **D:** At 0.23 s the bolus has passed to the larynx, and the epiglottic marker begins to ascend. **E:** At 0.29 s after time 1, the epiglottis is upright, the airway is again visible, and the swallow is complete.





sequence to see whether progressive changes occur. The duration of swallowing was brief, typically less than 0.5 s. The two species did not differ in swallowing duration, but in both swallowing was more rapid for liquid than for solid food. Individual variation was seen among the pigs, with pig 1 showing a shorter duration than the others. For solid foods the time interval between swallows was considerably longer than for successive liquid swallows (7–16 s vs. 0.6–0.7 s; statistics unnecessary). This is a reflection of the fact that solids need to be chewed prior to being formed into a bolus. The species did not differ in swallowing interval.

The time course of epiglottic movement is given in Table 2. Once at the inferior point of its movement, the epiglottis did not ascend immediately but remained depressed until the bolus had completely passed its downturned tip. The ranges for each stage of epiglottic movement were similar: descent 0.07–0.18 s, downturned 0.07–0.20 s; and ascent 0.06–0.21 s. Comparison of the three pigs swallowing hard chow reveals individual differences (pig 1 faster descent and pig 2 slower ascent). Within pig 1 and ferret 1, differences due to food type are also clear. For the ferret, all epiglottic movements were slower for hard chow than for liquid. For the pig, epiglottic ascent was slower for hard chow than for soft chow or liquid. Because there was individual variation among animals, interspecific comparisons may not be valid. Nevertheless, the data at hand strongly suggest that for both liquid and hard chow swallowing, the ferret epiglottis remains depressed for a shorter period of time than does the pig epiglottis.

Fig. 5. Digitized frames of pig 3 swallowing hard chow. See Fig. 1 for digitizing conventions. This pig had an easily visible hyoid bone (H) and a mandibular implant (M), which were digitized in addition to the markers (E1, epiglottic marker; S, soft palate marker) and reference points (V1 and V2, vertebral references). The base of the epiglottis (E2) is marked by an arrow in B–E. **A:** Rest position. **B:** At 0.12 s later, the hyoid is elevated, and the epiglottis depressed simultaneously with palatal elevation. **C:** At 0.20 s the epiglottis is maximally descended. **D:** Epiglottic ascent and hyoid descent are occurring at 0.30 s. **E:** Continued ascent of the epiglottis accompanies soft palate descent at 0.32 s. **F:** The swallow is complete at 0.36 s.

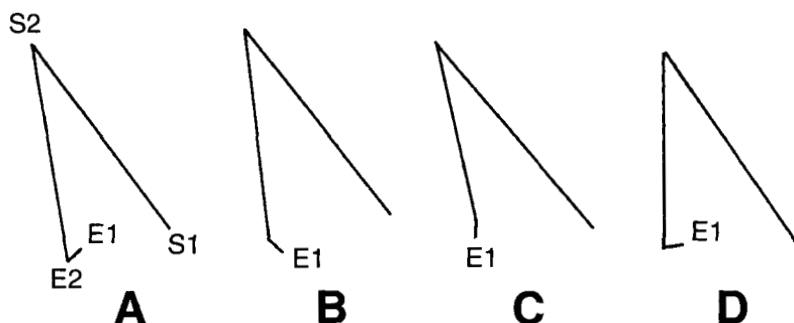


Fig. 6. Digitized frames of ferret 1 swallowing hard chow. See Fig. 2 for digitizing conventions. E1 and E2, upper and lower tips of the epiglottic marker; S1 and S2, skull reference points. **A:** The epiglottis is upright, just prior to the swallow. **B:** At 0.15 s later, the swallow begins with downturning of the epiglottis. **C:** At 0.25 s the epiglottis reaches maximum depression. **D:** By 0.40 s the epiglottis has returned to an upright position, completing the swallow.

## DISCUSSION

Our study indicates that the momentary unlocking of the larynx from the soft palate is in fact a downfolding of the epiglottis. The epiglottis folds down invariably and completely during swallowing in two diverse mammals, one of which is an ungulate, the group thought to epitomize the erect epiglottic morphology. This dramatic movement is independent of whether the bolus is liquid or solid. Although generalizing from these two species (plus adult humans) is speculative, we believe that this evidence strongly suggests that downfolding of the epiglottis during swallowing is the primitive condition for adult mammals. Adding this information on functional morphology to the previously reviewed data showing that breathing and swallowing do not co-occur, we conclude that the functional reorganization of the oral apparatus during the evolution of the genus *Homo* has not been as thorough as previously believed. The coordination and performance of swallowing in adult humans is essentially the same as in other mammals. Nevertheless, the remainder of the scenario laid out at the beginning of this article may be quite valid. The descent of the larynx during postnatal ontogeny is undoubted, and its explanation vis-à-vis speech sounds is still plausible.

It is interesting to compare the time course of epiglottic movement among species. Ardran and Kemp (1952) calculated the speed of movement of the human epiglottis to be 1

cm/20 ms or 0.50 m/s. In the pig the epiglottic marker descends through an arc of approximately 90 degrees. In a pig weighing 25 kg the epiglottis is approximately 30 mm long. This movement therefore represents a linear distance of 50 mm, resulting in a linear velocity of approximately 0.25 m/s or 8 radians/s. This is of the same order of magnitude as Ardran and Kemp's figure. Another similarity is the total duration of the epiglottic cycles for swallowing—0.3–0.5 s in both species, which compares favorably with the 0.5 s of airway closure given by Koenig et al. (1990) for human infants.

We note that a number of important issues remain. First, our study did not directly address whether pigs and ferrets are obligate nasal breathers or whether breathing actually ceases during swallowing. However, the resting posture of the epiglottis in both species implies that they are at least usual if not obligate nasal breathers. Furthermore, the depressed epiglottis during swallowing would block air intake substantially if not completely, so it seems likely that respiration is interrupted just as in rabbits (McFarland and Lund, 1993), which have similar laryngeal architecture to pigs, and in dogs (Bosma, 1957; Biewener et al., 1985), which have similar laryngeal architecture to ferrets.

A second issue is that our data do not speak to the question of infant animals. However, German and Crompton (1994) have observed barium swallows in infant

pigs and monkeys. They observed milk sometimes passing over the bent epiglottis only in piglets. In the monkeys the milk passed lateral to the epiglottis, but the airway was nonetheless occluded, at the nasopharyngeal level. Infant humans probably resemble infant monkeys, according to the literature summarized by Peiper (1963); specifically, the airway is occluded briefly even though the epiglottis may remain erect. Taxon-specific movement patterns but not physiological coordination are thus implied for infants.

Third, the mechanism of epiglottic depression remains to be analyzed. The fact that the hyoid and epiglottis moved in opposite directions during pig swallowing indicates that downfolding is not a simple raising of the larynx but a true inversion of the epiglottis. Further confirmation was supplied by the changing angulation of the linear profile of the epiglottic marker in both pigs and ferrets (Figs. 3–6). Many authors have speculated that pressure from the bolus causes epiglottic movement (reviewed by Fink and Demarest, 1978). Our data cannot disprove this notion, because a bolus was always present. On the other hand, several observations suggest that the bolus cannot be the only effector of epiglottic depression. For example, the epiglottis stayed in the downward position until very little if any of the bolus remained on its superior surface. If it were simply bolus pressure that maintained the epiglottis in its depressed position, then the epiglottis should begin ascending earlier. Further, epiglottic downfolding is complete even for small boluses. Another argument against the primacy of bolus pressure is the timing of epiglottic movement for liquid and solid boluses. Liquid swallows were actually more rapid in both species, and in the ferret epiglottic descent was much faster with liquids, suggesting that a large cohesive bolus is not required. An additional mechanism that may account for the full range of downturning in the muscle-poor epiglottis has been suggested by Fink and Demarest (1978), who have theorized that in humans differential pressure on the epiglottic cartilage produced by the adjacent structures can fold the upright epiglottis into a downturned conoid. Analogously, in other mammals the upward movement of the entire larynx may

cause forceful contact between the upright epiglottis and the soft palate, initiating the downturning which then continues by virtue of the intrinsic bending properties of the epiglottic cartilage itself.

The present study does not deny that the epiglottis may have evolved to help separate the respiratory and digestive pathways (Laitman and Reidenberg, 1993). However, the claim that adult humans are unique in using the epiglottis as a protective device during swallowing (Laitman et al., 1977; Sasaki et al., 1977) is probably incorrect in view of the very similar movement made in other mammals. If there is an adaptation for maintaining breathing while eating in mammals, it seems to be in the rapidity of the swallowing motion rather than in the ability of the epiglottis to maintain a patent airway by locking onto the soft palate while swallowing.

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## LITERATURE CITED

- Ardan GM, and Kemp FH (1952) The protection of the laryngeal airway during swallowing. *Br. J. Radiol.* 25:406–416.
- Ardan GM, Kemp FH, and Lind J (1958) A cineradiographic study of bottle feeding. *Br. J. Radiol.* 31:11–22.
- Biewener AA, Soghikian GW, and Crompton AW (1985) Regulation of respiratory airflow during panting and feeding in the dog. *Respir. Physiol.* 61:185–195.
- Bosma JF (1957) Deglutition: Pharyngeal stage. *Physiol. Rev.* 37:275–300.
- Bosma JF, Truby HM, and Lind J (1965) Cry motions of the newborn infant. *Acta Paediatr. Scand. Suppl.* 163:62–92.
- Crelin ES (1987) *The Human Vocal Tract*. New York: Vantage Press.
- Eckberg O, and Sigurjonsson SV (1982) Movement of the epiglottis during deglutition. *Gastrointest. Radiol.* 7:101–107.
- Fink BR, and Demarest RJ (1978) *Laryngeal Biomechanics*. Cambridge, MA: Harvard University Press.
- German RZ, and Crompton AW (1994) Integration of swallowing and respiration in infant mammals. *J. Morphol.* 220:348.

- Herring SW, and Scapino RP (1973) Physiology of feeding in miniature pigs. *J. Morphol.* 141:427-460.
- Johnstone AS (1942) A radiological study of deglutition. *J. Anat.* 77:97-100.
- Kenny DJ, Casas MJ, and McPherson KA (1989) Correlation of ultrasound imaging of oral swallow with ventilatory alterations in cerebral palsied and normal children: Preliminary observations. *Dysphagia* 4: 112-117.
- Koenig JS, Davies AM, and Thach BT (1990) Coordination of breathing, sucking, and swallowing during bottle feedings in human infants. *J. Appl. Physiol.* 69: 1623-1629.
- Kramer SS, and Monahan-Eicher P (1993) The evaluation of pediatric feeding abnormalities. *Dysphagia* 8:215-224.
- Laitman JT, and Crelin ES (1980) Developmental change in the upper respiratory system of human infants. *Perinatol.-Neonatal.* 4:15-22.
- Laitman JT, and Heimbuch RC (1982) The basicranium of Plio-Pleistocene hominids as an indicator of their upper respiratory systems. *Am. J. Phys. Anthropol.* 59:323-343.
- Laitman JT, and Reidenberg JS (1993) Specializations of the human upper respiratory and upper digestive systems as seen through comparative and developmental anatomy. *Dysphagia* 8:318-325.
- Laitman JT, Crelin ES, and Conlogue GJ (1977) The function of the epiglottis in monkey and man. *Yale J. Biol. Med.* 50:43-48.
- Lieberman P, Crelin ES, and Klatt DH (1972) Phonetic ability and related anatomy of the newborn and adult human, Neanderthal man, and the chimpanzee. *Am. Anthropol.* 74:287-307.
- McFarland DH, and Lund JP (1993) An investigation of the coupling between respiration, mastication, and swallowing in the awake rabbit. *J. Neurophysiol.* 69:95-108.
- Mosher HP (1927) X-ray study of movements of the tongue, epiglottis, and hyoid bone in swallowing, followed by a discussion of difficulty in swallowing caused by retropharyngeal diverticulum, post-cricoid webs and exostoses of cervical vertebrae. *Laryngoscope* 37:235-262.
- Negus VE (1949) *The Comparative Anatomy and Physiology of the Larynx*. London: W. Heineman Medical Books Ltd.
- Negus VE (1965) *The Biology of Respiration*. Baltimore: Williams & Wilkins Co.
- Nickel R, Schummer A, Seiferle E, and Sack WO (1973) *The Viscera of the Domestic Mammals*. Berlin: Verlag Paul Parey.
- Peiper A (1963) *Cerebral Function in Infancy and Childhood*. New York: Consultants Bureau.
- Ramsey GH, Watson JS, Gramiak R, and Weinberg SA (1955) Cinefluorographic analysis of the mechanism of swallowing. *Radiology* 64:498-518.
- Rushmer RF, and Hendron JA (1951) The act of deglutition: A cinefluorographic study. *J. Appl. Physiol.* 3:622-630.
- Sasaki CT, Levine PA, Laitman JT, and Crelin ES (1977) Postnatal descent of the epiglottis in man. *Arch. Otolaryngol.* 103:169-171.
- Saunders JB, Davis C, and Miller ER (1951) The mechanism of deglutition (second stage) as revealed by cine-radiography. *Ann. Otol. Rhinol. Laryngol.* 60:897-916.
- Selley WG, Ellis RE, Flack FC, and Brooks WA (1990) Coordination of sucking, swallowing and breathing in the newborn: Its relationship to infant feeding and normal development. *Br. J. Disord. Commun.* 25: 311-327.
- Siegel S, and Castellan NJ (1988) *Nonparametric Statistics for the Behavioral Sciences*, 2nd ed. New York: McGraw Hill.
- Sisson S, and Grossman JD (1953) *The Anatomy of the Domestic Animals*, 4th ed. Philadelphia: W.B. Saunders.
- Wilson SL, Thach BT, Brouillette RT, and Abu-Osba YK (1981) Coordination of breathing and swallowing in human infants. *J. Appl. Physiol.* 50:851-858.